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Incorporating territory compression into population models

Jo Ridley, Jan Komdeur and William J. Sutherland

Ridley, J., Komdeur, J. and Sutherland, W. J. 2004. Incorporating territory compression into population models. – *Oikos* 105: 101–108.

The ideal despotic distribution, whereby the lifetime reproductive success a territory's owner achieves is unaffected by population density, is a mainstay of behaviour-based population models. We show that the population dynamics of an island population of Seychelles warblers (*Acrocephalus sechellensis*) cannot be modelled with an ideal despotic distribution, and suggest the effects of both territory shrinkage and territorial disputes on reproductive success must be included to adequately model the population dynamics of this species. To do this we introduce two different approaches. The first is reductionist, using data on how population density affects individuals' reproductive success to predict population growth rates. Because such a model is mechanistic, it can be used to predict population dynamics in novel environments, making it a desirable long-term solution. However, because territorial populations are typically tightly regulated, birth and death rate data at low population densities are often unavailable. Hence, our second approach statistically infers the relationship between population density and per territory reproductive success, and thus provides a stop-gap solution for the shorter term. Our analysis indicates that although the Cousin population of Seychelles warblers is highly resilient to environmental stochasticity, the degree of resilience is considerably underestimated by approaches that ignore intrinsic regulation through territory shrinkage and territorial disputes.

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In order to predict the dynamics of populations, we must understand the density dependent processes through which population sizes are regulated. In many systems, breeding territories limit the number of individuals able to breed in an area, and so are central to population regulation. Examples of territoriality regulating population size come from mammals (Wolff 1997), birds (Newton 1998), fish (Barlow 1993, Balshine et al. 2001) and invertebrates (Baker 1983). Given their ubiquity, and also that they provided the inspiration for early attempts at linking behaviour to population regulation (Fretwell and Lucas 1970), it is initially surprising that behavioural models for these systems lag behind those for populations regulated while in

flocks (Sutherland 1996, Gill et al. 2001, Stillman et al. 2002).

Many of the behaviour-based models that link territoriality to population regulation models are relatively simple in that they assume territories are fixed quantities, with the owner of a given territory achieving the same reproductive success, independent of population density. All such models are versions of the ideal despotic distribution (Fretwell and Lucas 1970), and they predict two processes that regulate population size: as density increases, individuals may either move into poorer habitat (Rodenhous et al. 1997), or choose to delay breeding (Kokko and Sutherland 1998, Ridley and Sutherland 2002, Stephens et al. 2002). In reality, ideal

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despotic distributions may be too simplistic because territories are often highly fluid quantities (Watson and Miller 1971, Stamps 1994, Both and Visser 2000, Calsbeek and Sinervo 2002). Although Milinski and Parker (1991) noted a decade ago that ideal despotic distribution models needed developing to incorporate decreasing territory size as population density increases, to date little progress has been made.

In this paper we extend a model written to predict habitat occupancy by the Seychelles warbler (*Acrocephalus sechellensis*), for populations at demographic equilibrium (Ridley et al. 2003), to one which predicts population dynamics over all densities. We then examine how the plastic nature of territories tightens population regulation. This species bears many hallmarks of despotic behaviour, which suggests an ideal despotic distribution may be appropriate. Because an ideal despotic distribution fails for this species we suggest that such distributions may rarely exist outside theoretical models, and consequently that modelling interference competition in territorial populations is an area ripe for development.

The model

The life history, study site and methodology for the Seychelles warbler study have been covered in detail elsewhere (Komdeur et al. 1995). In brief, the Seychelles warbler is a cooperative breeding and insectivorous species, endemic to the Seychelles archipelago. Year-round territories are maintained; and on the basis of insect density, these can be divided into three quality classes: high, medium and low (Komdeur 1992). By the 1960s the entire world's population was confined to the island of Cousin (28 ha), and had been reduced to around 30 birds as a consequence of habitat destruction through coconut planting. All the birds were confined to a 2-ha undisturbed mangrove patch where they bred as simple pairs. Following habitat restoration, starting in 1968, the population increased, saturating the entire available habitat from 1973 onwards. As the habitat neared saturation, some of the offspring on the high and medium quality territories started to delay dispersal beyond reproductive maturity, such that familial groups formed (Komdeur 1992).

The non-breeding and use of poorer habitat that were observed as density increased are consistent with the predictions of the ideal despotic distribution, and in an earlier model we show that these processes are sufficient to explain the near-equilibrium population dynamics on Cousin (Ridley et al. 2003). However, to model the population dynamics at densities away from demographic equilibrium, there are at least two additional processes that may be important. Firstly, due to the process of territory budding, in which male sub-ordinate

breeders progressively acquire a territory for themselves, by taking ground from both their parents and their neighbours, territory areas decline with increasing population density (Komdeur and Edelaar 2001). This has the potential to deprive individuals of resources (Davies and Houston 1981), and there is evidence that this occurs in the Seychelles warbler (Komdeur and Edelaar 2001). Secondly, as space becomes a limiting resource, the energy spent on territorial disputes may increase (Stuartsmith and Boutin 1994). Consistent with this, as density increases and sub-ordinate females start to lay eggs in the dominant's nest (co-breed), they help their parents with both reproduction and territory defence.

Our existing model (Ridley et al. 2003) is an individual-based stochastic simulation in which offspring leave their natal territory when so doing maximises their inclusive fitness. In this model reproductive success depends on the density of insects (more insects leads to both higher fecundity and higher survivorship, Komdeur 1992), and the number of co-breeding females (with either 1 or 2 being optimal, Table 1). To extend this model for use away from demographic equilibrium, we also need to allow the fitness that territories offer to vary with density. To this end we derive 2 functions: one relating territory size to fitness and one relating the frequency of territorial disputes to fitness. In principle, reproductive success, for a given number of co-breeders in a given habitat area, could be altered with density through changes in both fecundity and survivorship. However, because fecundity is linearly related to lifetime reproductive success, but annual survival is not, for simplicity, we assume that only fecundity changes, and thus that the effect of density on lifetime reproductive success is constant across habitat types.

In the simplest scenario, territory sizes might be determined by simply dividing the available area of habitat between its occupant breeding pairs, and fecundity might be linearly related to territory size. However, we make two modifications to this simplest approach. First, consistent with the observed behaviour (Komdeur and Edelaar 2001), we assume an upper limit to the size of territory a pair can exploit, and also a lower limit beneath which territory sizes do not fall. We define the ratio of these two sizes as B , and the area of a territory as A . Accordingly:

$$A = \begin{cases} 1, & \frac{N_p}{T_s} \leq 1 \\ \frac{N_p}{T_s}, & 1 < \frac{N_p}{T_s} < B \\ B, & \frac{N_p}{T_s} \geq B \end{cases} \quad (1)$$

where N_p is the number of pairs attempting to breed in a habitat and T_s the number of territories recorded in each habitat at demographic equilibrium (i.e. 14, 20 and 89

respectively, in the high, medium and low quality habitat). Where $A = 1$ this corresponds to the territory sizes observed at demographic equilibrium on Cousin, i.e. approximately 250m^2 . We relate territory size to fitness by increasing per territory fecundity according to

$$M_{N,s} = M_K A^c \quad (2)$$

where c is a constant relating available resources to fitness, $M_{N,s}$ is fecundity with N birds in a habitat, s denotes territory shrinkage, and M_K is fecundity as measured for the population around its demographic equilibrium. Although M_K is not a constant, but varies with both the numbers of co-breeders and habitat quality (Table 1), we avoid adding additional subscripts to denote this for the sake of easier reading. The effect of territory shrinkage on fecundity is illustrated in Fig. 1.

We next derive a function for the fitness consequences of territorial disputes. If the energy spent on defending only a single boundary (i.e. if there were only 2 pairs of birds) means fecundity is reduced by a proportion δ , then fecundity must decline at least according to

$$M_{N,d} = M_{1,d}(1 - \delta)^{N-2} \quad (3)$$

$M_{N,d}$ is fecundity with N birds in a habitat where the number of territory disputes increases linearly with the number of territory boundaries. However, noting that co-breeders also participate in territory defence, we assume the cost of territory disputes increases, not just with the number of territory boundaries, but with the number of birds in a habitat, giving us the following closely related relationship

$$M_{N,d} = M_{1,d}(1 - \delta)^{f(N-1)} \quad (4)$$

where $f(\cdot)$ is an unspecified function. If $f(\cdot)$ is any linear function, we can make the following simplification

$$M_{N,d} = M_{1,d}D^{N-1} \quad (5)$$

where D is a parameter that incorporates both the cost of territorial disputes, and the rate at which their frequency increases with density. If K is the population

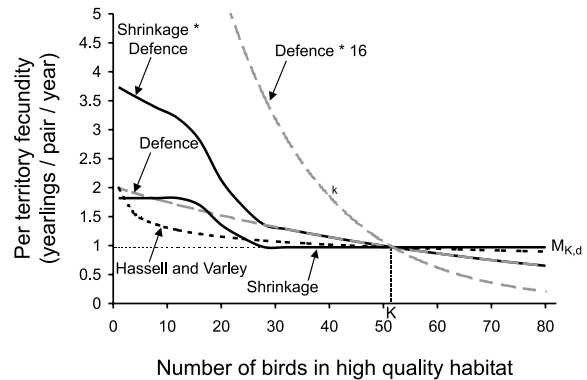


Fig. 1. Five relationships between fecundity and density; illustrated for the high quality habitat on Cousin. Territory sizes have an upper limit, due to the physiological constraints on individuals' capacity to utilise resources. They also have a lower limit, because below a certain territory size, it is both profitable for, and residents are capable of, preventing further shrinkage. Accordingly, where fecundity is linearly related to territory size, these processes combine to mean that fecundity is density independent at both low and high densities (line labelled 'shrinkage'). The line labelled 'defence' shows the density dependent decline in fecundity caused by territory defence used in our behaviour-based model, and that labelled 'defence $\times 16$ ' the relationship used where we statistically fit Eq. 5 to the observed population trajectory. The similar shapes of the composite 'territory shrinkage \times territory defence' function and the 'defence $\times 16$ ' function indicate we can adequately amalgamate the two behavioural processes into a single descriptive function. Also illustrated is the Hassell and Varley (1969) interference function, which describes a biologically analogous process to territory defence, but produces a more non-linear relationship with density than Eq. 5, and thus less tight population regulation.

size, for each habitat class at demographic equilibrium (Table 1), we rearrange Eq. 5 for D ,

$$D = \left(\frac{M_K}{M_{1,d}} \right)^{1/(k-1)} \quad (6)$$

meaning that, as we have the demographic equilibrium parameters: M_K and K (Table 1), we only need $M_{1,d}$ to solve for D .

Table 1. Bird densities at demographic equilibrium (Komdeur 1992) and the effect of co-breeders on annual production of yearlings (Komdeur 1994) detailed by habitat quality (Komdeur 1992). Large numbers of helpers decrease fecundity, resulting from increased risk of egg break caused by simultaneous incubation by more females, and greater depletion of food resources. (Komdeur 1994). As we lack sufficient data for fecundities for large group sizes, these were assumed to decline by a constant parameter (70%), the fraction by which a second helper decreases fecundity on medium quality territories. 'helpers - 1 fec' denotes the per territory fecundity with one less helper. Data was collected during a continuous study from December 1985 to June 1991, during which period nearly the entire population was colour ringed, and censused.

Territory quality	Number of birds	Number of co-breeders			
		0	1	2	> 2
High (sample size)	52	0.97 (28)	1.55 (13)	1.99 (11)	$0.7 \times (\text{helpers} - 1 \text{ fec})$
Medium (sample size)	58	0.50 (38)	1.51 (12)	1.04 (6)	$0.7 \times (\text{helpers} - 1 \text{ fec})$
Low (sample size)	214	0.20 (286)	0.32 (49)	0.12 (26)	$0.7 \times (\text{helpers} - 1 \text{ fec})$

A second potential function, for the fitness consequences of territory defence, can be derived by noting that territory defence is an analogous process to interference among feeding individuals, in that individuals waste energy on fighting each other. Interference has frequently been modelled using the Hassell and Varley (1969) function:

$$M'_{N,d} = M_{1,d}(K - 1)^{-m} \quad (7)$$

where m measures the strength of interference. Similarly to above, we can rearrange to solve for m , again leaving $M_{1,d}$ the only unknown:

$$m = \frac{-\ln\left(\frac{M_K}{M_{1,d}}\right)}{\ln K} \quad (8)$$

Results

The behaviour-based approach

We are seeking a parsimonious model, which can predict the population dynamics of the Cousin population of Seychelles warblers, in both saturated and unsaturated environments. Given this objective, we first try our 'equilibrium model' (Ridley et al. 2003), which is an ideal despotic distribution in that it ignores any fitness effects of territory shrinkage or territorial disputes. This model indicates that cooperative breeding should start at a much lower density than was observed (Fig. 2). The equilibrium model also predicts an unrealistically low rate of population increase (Fig. 2). At low population densities, additional group members, beyond the basic pair are less desirable than at high densities. Such density dependence in the benefit of group living is likely to be due to the participation of co-breeders in territory defence, and the increasing importance of territory defence as space becomes limiting. This suggests that a given territory yields higher reproductive success at lower densities, and thus that shrinkage and/or disputes are important to the population dynamics on Cousin.

Next we see if the observed pattern of territory shrinkage can, by itself, provide a sufficient explanation for this discrepancy, i.e. using Eq. 2 to vary fecundity with density. When birds were first translocated to Aride, territories were 1.81 times larger than their size in a saturated habitat of similar quality (Komdeur and Edelaar 2001), i.e. $B = 1.81$. If fecundity were linearly related to territory size, c would be one, but this also results in a rate of population increase that is slower than the observed rate (Fig. 2). In fact, starting with 30 birds in 1968, to match the population size observed in 1975 c must be 3.6, i.e. for a given habitat, a doubling of territory size leads to offspring production that is twelve times higher. Such an extreme relationship between the quantity of resources available and offspring production

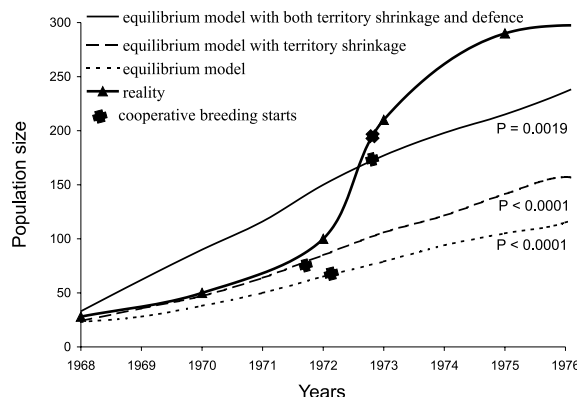


Fig. 2. A comparison between the population growth rate predictions for 3 increasingly complex models and the actual population trajectory (solid line with triangles) for the Cousin population of Seychelles warblers. Bold crosses indicate the start of cooperative breeding estimated by averaging over 100 model runs. The P value associated with each line is the probability its gradient is significantly different from that of the reality line, with linear regression used in all instances. An 'equilibrium model' (dotted line) assuming that birth rates do not vary with bird density in a habitat, despite successfully predicting equilibrium habitat occupancy (Ridley et al. 2003), underestimates the population growth rate and predicts cooperative breeding starting earlier than was observed by Komdeur (1992). Incorporating the fitness effects of territory shrinkage (dashed line) improves these predictions only marginally. Incorporating the combined fitness effects of territorial disputes and territory shrinkage (solid line) further improved the prediction, though cooperative breeding still tended to start a little early, and population growth was smoother than observed, but otherwise similar. Incorporating the habitat improvement, initiated in 1968, would yield a better fit to the S-shaped line depicting reality.

seems highly improbable. This does not mean that offspring production is not substantially higher on larger territories, indeed it is the central point of this paper that it is. However, we suggest that this relationship between density and fecundity cannot be explained on the basis of resource availability alone, but must also be due to the higher costs of defending resources at higher bird densities. Similarly, territory shrinkage by itself cannot provide a density dependent benefit for group living, and thus the relatively late onset of cooperative breeding (Fig. 2).

Accordingly, we add the effect of territorial disputes, such that fecundity is given by the product of Eq. 2 and 5. Unfortunately, we lack data for the parameter necessary to do this: $M_{1,d}$, and so have to estimate it. To do this we assume that a pair in an unsaturated environment could achieve the same fecundity as the optimum-sized group can in a saturated environment, where an 'optimum-sized group' has the number of helping offspring that maximises per territory fecundities (Table 1). This amounts to assuming that retained offspring offset the increasing cost of territorial disputes at high densities. The effect of territory defence on fecundity, under this assumption, is illustrated in Fig. 1.

If $c = 1$, this approach produces cooperative breeding and a population growth rate close to that observed (Fig. 2).

The statistical approach

A more pragmatic approach to estimating the maximal rate of fecundity ($M_{1,d}$) in this, or any similar system, is to infer it statistically from the observed rate of population increase. To do this, we first assume that the effect of territory shrinkage on fecundity can be subsumed within a function intended to describe the effects of territorial disputes. This means that we have a single function, describing how per territory fecundity changes with the density in a given habitat, that contains only one unknown parameter: $M_{1,d}$. We can then vary this parameter so as to fit the model to the observed population dynamics.

We do this for both our own territory defence function (Eq. 5) and also the Hassell and Varley (1969) function (Eq. 7) by assuming that, for a given habitat, maximal fecundity ($M_{1,d}$) is greater than fecundity at demographic equilibrium (M_K , Table 1) by a term g , which is constant across habitats. I.e. $gM_{K,d} = M_{1,d}$, and thus $D = 1/g^{1/(K-1)}$ and $m = \ln(g)/\ln(K)$. We then find the value of c that minimise the sums of square deviations between the model predicted, and the observed population increase between 1970 and 1975 (Fig. 2). We start in 1970 so as the benefits of habitat restoration had had the opportunity to feed through. For our own territory defence function (Eq. 5) a value of $g = 16$ best fits the data. Whilst this is large, for the Hassell and Varley function a g of around 10000 produces the best fit. A precise value for g is hard to obtain because the sums of squares deviation does not reach a clear minimum value.

Territory compression and extinction threat

To illustrate the importance of including the fitness effects of territory compression in population models we contrast the extinction risk predicted by our original ideal despotic distribution based model (Ridley et al. 2003) with that predicted where territory compression effects are included. To do this, we note that in 1997 all nests on Cousin were destroyed by an El Niño related storm, and thus we assess the relationship between the frequency of zero-fecundity years and time to extinction (Fig. 3). This analysis indicates that, although the Cousin population is exceptionally resilient to this form of environmental threat, the degree of this resilience is strongly underestimated if territory compression is ignored. Further, though our behaviour-based and statistical approaches produce very different estimates of maximal fecundity (y-intercepts in Fig. 1), extinction risk is relatively insensitive to this variation.

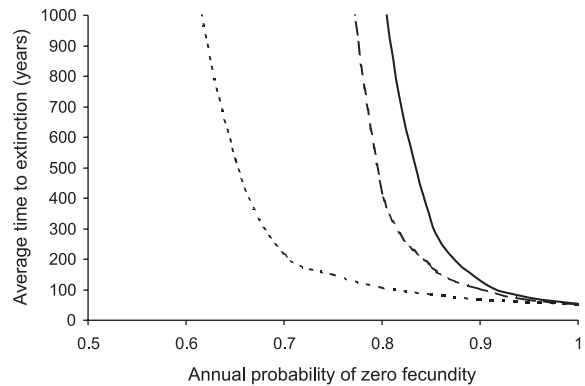


Fig. 3. Three relationships between time to extinction and environmental stochasticity, defined as the annual probability fecundity is zero, as occurred in 1997 due to El Niño storms. All models predict the extinction threat posed by El Niños is remote: they need to occur in 3 out of every 4 years to become a significant threat. However, a model without territory compression (Ridley et al. 2003; dotted line) predicts a markedly higher extinction risk, than models that do incorporate it: using either the available data (dashed line), or a statistical approach (solid line). The statistical model indicates fecundity at very low densities would be 16 times higher than it is on the same territory, when the population is at demographic equilibrium, whereas the available data indicates it could be 4 times higher. This large difference translates into a much smaller difference in the extinction predictions. Though we only make comparisons with the extinction threat posed by environmental stochasticity in the form of El Niño storms, and other threats, such as epidemics, would clearly be sufficient to drive the population extinct, this does not alter our analysis that this population is exceptionally tightly regulated. Times to extinction are estimated as the average of 100 model runs, with runs starting from the current demographic equilibrium (~ 320 birds).

Discussion

For a population to be viable, we know that at demographic equilibrium, an average territory must offer a lifetime reproductive success of one, and that at lower densities lifetime reproductive success must be more than one. If birds are 'free' in the sense of Fretwell and Lucas (1970), all individuals have equal fitness, and thus all territories must offer identical lifetime reproductive successes. Accordingly in 'free' territorial systems all the density dependence must arise through a density dependent decline in the lifetime reproductive success each territory offers. At the opposite extreme, if birds are capable of complete despotism, bird density will have no effect on the lifetime reproductive success of resident birds' territories. This implies that as density increases, all the population regulation will arise through individuals choosing to: (1) breed on poorer territories and (2), delay breeding (either as floaters or subordinate residents).

The data needed to model density dependence in territorial systems thus depends on where species sit on the continuum between these 'free' and 'despotic' extremes. For an exceptionally despotic species we could

use data on birth and death rates as measured around demographic equilibrium to predict population dynamics at low densities. By contrast, such an assumption for any other species would underestimate the strength of density dependent responses to environmental stochasticity. This is a particular problem, given that territorial species are typically tightly regulated, and thus we often only have data for populations around demographic equilibrium.

Territorial populations are density dependent

We have established a robust case for lifetime reproductive success on a given territory changing with density in a highly despotic species. Firstly, although the forms of the functions we have used to link territory shrinkage and defence to fitness are simple in their form, and so unlikely to precisely represent the actual behaviours, we believe that they are qualitatively right. Firstly, smaller territories do produce fewer recruits (Komdeur et al. 1995), with warbler pairs on Aride initially producing offspring 23 times as fast as warbler pairs on Cousin (Komdeur 1996). This is because warblers on Aride produced twins and bred year round, whereas warblers on Cousin produced mainly single chicks only once per year. Secondly, without territory compression, population growth rates are significantly less than observed (Fig. 2), suggesting there must be some form of negative density dependence in addition to the sink usage and non-breeding predicted by our 'equilibrium' model (Ridley et al. 2003).

That the Seychelles warbler shows evidence for density affecting per territory reproductive success contradicts two recent perspectives on territorial populations. Using the restricted definition, that 'density dependence' only describes those processes that mechanistically depend on density (i.e. not resource limitation), Hunt and Law (2000) argue that territorial populations are 'not necessarily' and White (2001) that they are 'not' subject to density dependence. They, in effect, advocate the ideal despotic distribution model, whereby territorial systems comprise a fixed array of territories of fixed quality, and thus argue that reproductive success declines with increasing density because poorer habitat is occupied making density a correlate not a cause of declines in mean fitness.

The Seychelles warbler bears all the hallmarks of a highly despotic species: there is high variance in fitness both within (Richardson et al. 2001) and among habitat types (Komdeur 1992), and sub-ordinates typically leave their natal territories following the establishment of a new breeder (Komdeur 1999). That per territory reproductive success depends on density in the highly despotic Seychelles warbler suggests it also will in more 'free' systems. Evidence from other species, of both per

territory reproductive success depending on density (Stamps 1990, Calsbeek and Sinervo 2002), and of aggressiveness strongly impacting on population dynamics (Mougeot et al. 2003) further suggest that ideal despotic distribution models of territorial systems may rarely be sufficient to model the population dynamics of territorial species. Adopting White's (2001) perspective, that territorial populations are simply limited by resources, where in reality they also regulate themselves, will overestimate both the benefits of resource supplementation, and the risks of extinction.

This study also illustrates how density dependence mechanisms vary with spatial scale. Elsewhere we have shown that there is density dependence operating across habitat types, i.e. progressive occupancy of poorer habitats, which explains the size at which the Cousin population is stable (Ridley et al. 2003). In this paper we have now shown that there is also density dependence operating within habitat classes, through territory shrinkage and territory defence and it is this that explains the rate of population increase. One consequence of this is that models based only on birth and death rates in a stable population, would overestimate the threat posed by loss of the better habitats on Cousin, because the low quality habitat on Cousin is a pseudo-sink (Watkinson and Sutherland 1995), i.e. lifetime reproductive success is less than one at demographic equilibrium, but more than one at low densities. Accordingly, even if only the low quality habitat remained, a small population would persist.

The way forward

How we incorporate the plastic nature of territories into population models remains a challenge. The interdependence between individuals' dispersal decisions, and the lifetime reproductive success territories offer, makes the bottom-up prediction of how the value of territories to their occupants changes with density a formidable challenge. We would propose a two-pronged assault. In common with Adams (2001) and Gordon (1997), we advocate the development of mechanistic models which predict territory compression from fitness-maximisation criteria. To this end it has already been shown that habitat manipulations can be used to measure how territories change in size (Calsbeek and Sinervo 2002) and how such changes relate to fitness (Both and Visser 2000), and further how the costs of territory defence can be measured (Stuart-Smith and Boutin 1994).

In the shorter term, a more pragmatic approach is required, and we suggest that our statistical approach, which involves subsuming territory shrinkage within a territory defence function, may be a reasonable approximation. Firstly, the processes we partition as defence and shrinkage incorporate a multitude of interacting

behaviour. For instance extra-pair copulation rates increase with the local density of males, meaning more energy is spent on mate guarding (Komdeur et al. 1999), whilst where resources are in shorter supply, more time is spent foraging and less is spent guarding nests, resulting in higher predation by fodies (*Foudia sechellarum*, Komdeur and Kats 1999). Secondly, the distinct fitness profiles for shrinkage and defence (Fig. 1) is an exaggeration, due to our territory shrinkage function in effect assuming a step change from an ideal free to an ideal despotic distribution, once the equilibrium population size is reached.

Given this perspective, one way forward would be to statistically fit functions which might describe territory defence, across a range of species, and attempt to correlate life histories to the fitted parameters. In this light, we note that the results we obtained for the Hassell and Varley (1969) function ($g > 10\,000$) indicates that the initially steep, but subsequently flat form of this function (as illustrated in Fig. 1) is probably inappropriate for modelling territory defence. Further, because the Hassell and Varley (1969) function produces most density dependent change in fitness at low population sizes, it contrasts with the recently-confirmed received wisdom for K-selected species (Sæther et al. 2002). Furthermore, for 3 of the 6 species to which Hassell and Varley (1969) fitted their function, Eq. 5 yields an improved fit (higher R^2).

Conclusion

Here we have illustrated what we do not know: how territory shrinkage and territorial disputes affect fitness; and what we do know: ignoring this will undermine population models for most, if not all, territorial species. Twenty years ago one of us showed (Sutherland 1983) how the Hassell and Varley (1969) function could be combined with the ideal free distribution of Fretwell and Lucas (1970) to predict the population consequences of interference competition. This approach has now been developed to the point where realistic models for interference's consequences can quickly be derived for additional species (Stillman et al. 2002). Here we have suggested territory defence is an analogous problem that is awaiting similar resolution. As a first step, we have derived a simple density dependent function to describe the fitness consequences of territory defence, whilst retaining a biological basis for its form. This required two simplifying assumptions: territorial disputes increase linearly with density, and maximal fecundity is linearly related, across habitat types, to fecundity at demographic equilibrium. Determining whether this approach is adequate, or needs further development, provides a clear path forward for behaviour-based models of territorial species.

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